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ROS Regulation Mechanism for Mitigation of Abiotic Stress in Plants

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Abstract

Plants respond to various stresses during their lifecycle among which abiotic stress is the most severe one comprising heat, cold, drought, salinity, flooding, etc. which take a heavy toll on crop yield worldwide in every corresponding year. ROS has a dual role in abiotic stress mechanisms where, at high levels, they are toxic to cells while at the same time, the same molecule can function as a signal transducer that activates a local as well as a systemic plant defense response against stress. The most common ROS species are Hydrogen peroxide (H_2O_2), Superoxide anions (O_2^-), Hydroxyl radicals (OH^\cdot), and Singlet oxygen (1O_2) which are results of physiological metabolism often controlled by enzymatic and non-enzymatic antioxidant defense systems. ROS generally accumulate in plants during abiotic and biotic stress conditions resulting in oxidative damage which ultimately leads to programmed cell death. Many ROS scavenging pathways have been well studied against stress responses. Through careful manipulation of ROS levels in plants, we can enhance stress tolerance in plants under unfavorable environmental conditions. This chapter presents an overview of ROS regulation in plants and the essential enzymes involved in the abiotic stress tolerance mechanisms which are thoroughly discussed below.

Keywords: Plants, ROS, Abiotic stress, Signal transducer, antioxidants

1. Introduction

Drought, temperature, salinity, flooding and heavy metal toxicity are the examples of abiotic stressors. These multiple abiotic stressors sometimes occur at the same time [1, 2] and cause significant reduction in crop production. To satisfy the demands of food security for sustainable development in the era of a rising population and climate change, scientists predict a vital need for a "second green revolution" to produce higher yield and yield stability under non-optimal and adverse growing conditions through a combination of approaches based on recent advances in functional genomics [3, 4]. Plants have evolved a range of biological and biochemical responses to coping up with adverse climatic conditions, including the activation of many stress-responsive genes and the synthesis of different

structural proteins via complex signaling pathways, to confer resistance to abiotic stress conditions [5]. Reactive oxygen species (ROS) are byproducts of plant metabolic processes and are produced in a range of cellular compartments including chloroplasts [6], mitochondria [7], and peroxisomes [7, 8]. ROS not only cause irreversible DNA damage and cell death, but they also serve as important signaling molecules, regulating growth in plants under stress conditions. This suggests that ROS plays a dual role in vivo depending on their level of reactivity, production site, and ability to penetrate the cell membrane [9]. Reactive oxygen species (ROS), which include hydrogen peroxide (H_2O_2), superoxide radical ($O_2^{\bullet-}$), hydroxyl radical (OH^{\bullet}), and singlet oxygen (1O_2), are harmful byproducts of basic metabolic processes in living organisms [9, 10]. In plants, oxygen (O_2), the source of all ROS, is stable and not very reactive [11]. Many excellent reviews have focused on ROS metabolism [9, 12], ROS sensory and signaling networks [9, 13, 14], and the involvement of ROS in developmental and stress response processes [12, 13]. The majority of these reviews, however, provided an overall retrospective for the model plant *Arabidopsis*. [15] They discussed enzymatic and non-enzymatic antioxidants and their roles in abiotic stress responses. However, the anti-oxidant system's regulation mechanisms, or even the key components involved in ROS regulation and abiotic stress resistance, has yet to be compiled in crop plants. In this chapter, we provide insight into current knowledge on the regulation of ROS homeostasis in crop plants. The genes that have been recognized in ROS homeostasis regulation affecting abiotic stress tolerance in crop plants were summarized in particular.

2. ROS role in plant growth and development

Despite the continuous efforts and gains made in agriculture development during recent decades, many stress factors continue to harm the crop growth and productivity. Most of the crop plants thrive in suboptimal environmental surroundings. Stressful conditions are the main factor preventing them from exhibiting their maximum genetic competence in terms of growth and reproduction, and as a result, plant productivity suffers as an outcome of these aberrant circumstances [15–17]. These pressures resulted in significant productivity and economic declines around the world. These stresses might be either biotic or abiotic. Pathogens (viruses, bacteria, and fungi), insects, herbivores, and rodents are all examples of biotic stresses. On the other hands, drought (water scarcity situation), salinity (high concentration of salt), cold (chilling and frost), heat (high temperature), flooding (water excess), radiation (high-intensity ultraviolet and visible light), contaminants, and toxins (heavy metals, pesticides, and aerosols), and soil nutrient deprivation are all examples of abiotic stresses [16, 18]. Any of these conditions either separately or in combinations may have varying degrees of influence on plant growth and development (**Table 1**).

Environmental factors influence plant growth and development through morphological, physiological, biochemical, and molecular alterations. The plant organelle metabolic paths are vulnerable to variation in environmental factors [13]. Tolerance can be attained by plant breeding or cultural activities that mitigate damages and require knowledge of the plant's stress response and how it affects individual plants and plant processes [42]. Various mechanisms linked with abiotic stress instruct plant cells to develop oxygen radicals and their derivatives referred to as reactive oxygen species (ROS). Furthermore, the development of reactive oxygen species (ROS) is a crucial mechanism in higher plants, since it is used to relay cellular signaling information in reaction to fluctuating environmental conditions.

Stress type	Plant Sp.	Stress condition	Loss result	Reference
Salinity	Soybean (<i>Glycine max</i> L.)	Application of (0, 33, 66 and 99 mM NaCl)	Significantly ↓ shoot length by 24%, 32% and 47% , and shoot and dry weight by 46%, 61% and 80% and 44%, 65% and 83% at 33, 66 and 99 mM NaCl respectively and root fresh, dry weight by 23%, 20% and 53%, 53% at 66 and 99 mM NaCl respectively	[19]
	<i>Miscanthus × giganteus</i>	NaCl concentrations (0, 2.86, 5.44, 7.96, 10.65, 14.68, 17.5, 19.97 and 22.4 dS m ⁻¹)	Significantly ↓ biomass yield by 50% at 10.65 dS m ⁻¹ NaCl, root dry weight reduced by 61% at 22.4 dS m ⁻¹ NaCl	[20]
	Maize	0, 60, 120, 180 and 240 mM NaCl	Significantly ↓ in germination percentage (77.4%), germination rate (32.4%), length of radicle (79.5%) and plumule (78%), seedling length (78.1%) and seed vigor (95%) are obtained in highest level of salinity (240 mM)	[21]
	Tomato	1% and 3% NaCl	Significantly reduction in germination percentage 77.60% at 3% NaCl,	[22]
	Egg plant cultivars - Lagra Negra (LN), China-A2 (CH) and Black Beauty (BB)	NaCl (0, 50, 100, 150 and 200 mM)	Significantly ↓ survival of cultivar at 100 (50, 40, 30%), 150 (15, 0, 0) and 200 (0, 0, 0% or no survival of the plants)	[23]
	Lentil (<i>Lens culinaris</i> Medik.)	100 mM NaCl for 4 days	Significantly ↓ the growth (33%) and seedling fresh weight (44%)	[24]
Water logging	Maize var. DH605 and ZD958	Waterlogging for 3 and 6 days at third extended leaf stage (V-3, V-6), six extended leaf stage (V-3, V-6) and 10th day after flowering stage (10VT-3, 10VT-6), no waterlogging (CK)	Grain yields of DH605 in treatments V3-3, V3-6, V6-3, V6-6, 10VT-3 and 10VT-6 are 18.6 %, 30.3 %, 12.6 %, 18.8 %, 5.7 % and 13.9 % lower than in the control (CK), respectively. ZD958 yields in treatments V3-3, V3-6, V6-3, V6-6, 10VT3 and 10VT-6 are lower than CK yields by 15.6 %, 30.4 %, 13.0 %, 21.4 %, 5.9 % and 12.8 %, respectively	[25]
	Wheat	Waterlogging for 14 days at 22 days after sowing	Shoot dry weight ↓ by 37% and grain yield by	[26]

Stress type	Plant Sp.	Stress condition	Loss result	Reference
			32% compared with the non-waterlogged plants	
	Mung bean (<i>Vigna radiata</i>) var. MH-1K-24	Waterlogging at vegetative stage (30 days after sowing) for 3, 6 and 9 days	Photosynthetic loss at 3, 6 and 9 days are 43, 51, and 63 %, respectively, while grain yield loss was 20, 34 and 52 % respectively.	[27]
	Chinese kale (<i>Brassica oleracea</i> var. <i>alboglabra</i>) and Caisin (<i>Brassica rapa</i> subsp. <i>parachinensis</i>)	Waterlogging or water deficit for 19 days in case of Chinese kale and 14 days in case of Caisin	Significantly ↓ plant fresh (90%) and dry weight (80%), leaf area (86%) and leaf number (38%) in Chinese kale; no impact on leaf number in Caisin but ↓ plant fresh and dry weights and leaf area by 60–70%	[28]
Drought/ Water deficit	Wheat	Plants are kept at normal day/ night (21/ 15°C) temperature and moisture content was maintained at 30% field capacity	Grain yield reduced by 53.05% compared to control	[29]
	Eggplant cultivars - Lagra Negra (LN), China-A2 (CH) and Black Beauty (BB)	Drought stimulated by PEG (0, 3, 8 and 10%)	↓ survival of cultivar at 3 % (90, 75, 70%), 8% (60, 45, 40%) and 10% (10, 0, 0% survival)	[23]
	Black gram (<i>Vigna mungo</i> L.) cultivar T9, KU-301 and green gram (<i>Vigna radiata</i> L.) cultivar Pratap, SG21-5 SG 21-5	A temporary rain shed are constructed in the field with PVC (polyvinyl chloride) film (of about 0.15 mm thickness and 85% of transmittance) to avoid rainfall	↓ Seed yield (T9-31.28%, KU 301-48.52%, Pratap-37.12%, SG 21-5- 56.98%)	[30]
	Tomato genotypes viz., LE 1, LE 27, LE 57, LE 114, LE 118, LE 125, CO 3, PKM 1, TH CO 2 and TNAU TH CO 3	25 days old seedlings were transplanted and drought was imposed at first day after transplanting onwards based on IW/CPE, 0.5 IW/CPE for drought stress and 1.0 IW/CPE for control are maintained by irrigation the field at regular interval based cumulative pan evaporation.	Overall yield loss of tomato fruits up to 52 per cent under field condition, highest yield loss of 83.18 and 81.51 per cent are shown by LE 125 and LE 1 respectively.	[31]
Toxic/ heavy metals	Wheat	CdCl ₂ .H ₂ O (98%) @ 0, 5, 20, 50 and 80 mg L ⁻¹	Significantly ↓ in root length (70.4%), shoot length (81.2%), percent germination (68%) and germination index (76.8%) at 80 mg L ⁻¹ Cd compared to control	[32]

Stress type	Plant Sp.	Stress condition	Loss result	Reference
	Maize	CuSO ₄ ·5H ₂ O @ 0, 1, 10, 100, 1000, 5000, 10000 µmol/L in Hoagland culture medium	Significantly ↓ root activity in 1 µmol/L (18.3%), 10 µmol/L (62.7%), and then decrease slowly-slowly	[33]
	Maize (<i>Zea mays</i> L.) cultivars Run Nong 35 and Wan Dan 13	Cd (0, 75, 150, 225, 300, 375 µM)	Grain yield is reduced in the range of 4–11 % under different Cd toxicity levels	[34]
	Tomato (cultivar PKM –1)	ZnSO ₄ ·7H ₂ O (0, 50, 100, 150, 200 and 250 mg kg ⁻¹ soil)	Significantly ↓ in root length 21.86, 25.40 and 33.3 and shoot length 7.46, 26.73, 31.72%, leaf area 29.53, 45.79, 48.02, root dry weight 27.46, 37.20, 54.37 and shoot dry weight 16.78, 32.91, 41.86% @ 150, 200, 250 mg/kg ⁻¹ respectively	[35]
	Pepper (<i>Capsicum annuum</i> L.)	0.1mM PbCl ₂ and 0.1 mM CdCl ₂	Significantly ↓ in total dry mass, root dry mass and shoot dry mass under both heavy metal and in combination compered to control	[36]
	Bean (<i>Phaseolus vulgaris</i>)	Pot soil contaminated with As (III) 20, 50 mg/kg and As (V) 20, 50 mg /kg	Significantly ↓ in shoot dry weight (40.85%) in As (V), shoot biomass in As (III) 49.3% & As (V) 63.88%, Dry matter yield of roots in 20 mg/kg As (V) 34.42, 46.18, 59.87 and 50 mg/kg As (V) 43.82, 56.09, 71.67%	[37]
Heat stress/ High temperature	Maize	In pot trial 32/22 °C (max/min temperature, control), 36/26 °C, and 40/30 °C for 14 consecutive days bracketing flowering	At 40/30 °C grain yield, seed-set, and grain number significantly ↓ by 73.6, 76.4, and 77.6%	[38]
	Wheat	In field condition during hot area in Iran	Significantly ↓ in grain yield (46.63%), 1000-kernel weight (20.61%) and grain filling duration (20.42%)	[39]
	Soybean	Double crop growing season in field	Significantly ↓ seed yield (29.5%) compare to previous year	[40]
	Field pea (<i>Pisum sativum</i> L.);	Field pea crop exposed three distinct windows normal, moderately and late sowing to heat stress environment	Significantly ↓ in seed set (7–14%) and 100-seed weight (6–16%)	[41]

Table 1.
Effect of various abiotic stresses on plant growth, development and production.

As the crop yield is depending on the plant's capability to respond to various forms of environmental stresses, most of which causes oxidative stress and increases concentration of reactive oxygen species (ROS). Increased ROS accumulation is closely related to increased environmental stress. A variety of biotic and abiotic factors can disrupt the balance between ROS production and the scavenging process, and responsible for raising their levels in intra-cellular [10]. All of these are accountable to cause serious oxidative injury to the plants, limiting their growth parameters and revenue ultimately (**Figure 1**).

Reactive oxygen species (ROS) also play a role in a variety of processes, including cell growth, production, and comeback to biotic and abiotic environmental inducements, as well as programmed cell death and signal transduction. Stressors, hormones, growth, and a variety of additional metabolic pathways can all arouse ROS formation, which can then trigger other pathways or serve as direct defense compounds in the plant body [43]. But, when ROS synthesis exceeds cellular scavenging potential, it disturbs the cellular redox homeostasis and produce ROS [44, 45]. To counter these stresses, plants have antioxidant pathways that scavenge excess ROS and avoid cell damage. Thus, plant synthesis and quenching are out of equilibrium, resulting in yield losses due to oxidative disruption. Though, it is difficult to identify this drop to oxidative damage due to the many processes involved in ROS synthesis; however, stresses and oxidative damage are interconnected and are liable for yield reduction [46].

Therefore, understanding the oxidative appliances in plants might be an aid in the growth of plants that are best suited to their surroundings. Plants stimulate antioxidant defense mechanisms in response to stress, which helps in the continuation of cell constituent's structural integrity and, potentially reduces oxidative injury. Plant defense is aided by several antioxidant enzymes. As a result, maintaining a high antioxidant ability to abolish toxic levels of ROS has been concurrent to improved crop plant capacity towards stress tolerance.

Manipulating ROS scavenging enzyme organizations is a likely method for producing transgenic plants that are more tolerant to a variety of stress situations;

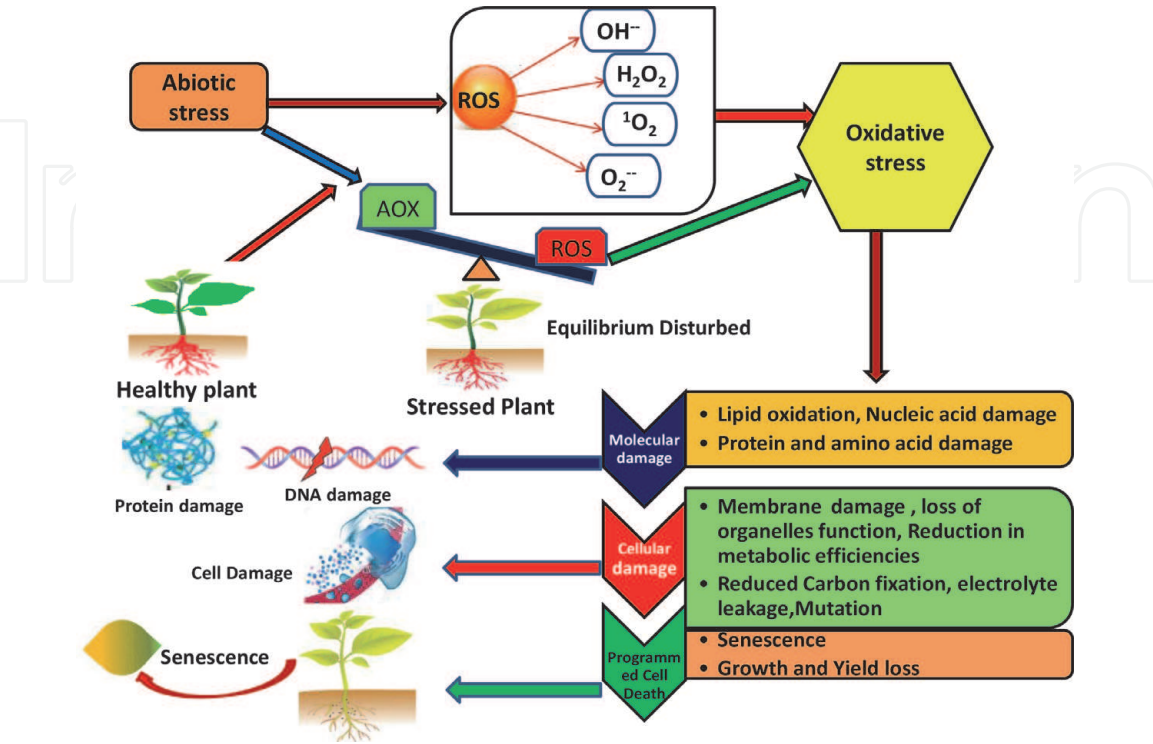


Figure 1.
Effect of oxidative stress on plant growth. ROS (Reactive oxygen species), AOX (Antioxidants).

however, more research is needed for this since many enzymes and isoforms are involved, and ROS is only one of the promising issues of plant tolerance to environmental and biotic stresses [47].

2.1 Plant antioxidant defense system overview

To minimize possible harm to cellular components, as well as to sustain growth, metabolism, development, and total yield, the balance between ROS generation and removal at the intracellular level must be closely controlled and/or competently processed. Antioxidants scavenge ROS and/or regulate ROS development, either directly or indirectly [48]. This antioxidant defence system comprises low-molecular-weight non-enzymatic antioxidants and some antioxidant enzymes [49]. Non-enzymatic components include tocopherol, carotenoids, phenolic compounds, flavonoids, alkaloids, and non-protein amino acids, besides cellular redox buffers like ascorbate (AsA) and glutathione (GSH) [50–52].

Numerous antioxidant enzymes, like superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), peroxidase (POX), polyphenol oxidase (PPO), peroxiredoxins (PRXs), Thioredoxins (TRXs), and ascorbate-glutathione (AsAGSH) cycle enzymes, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) are the parts of the enzymatic components of the antioxidant defense organization [53–56]. The above non-enzymatic antioxidants function in combination with antioxidant enzymes to keep the balance between ROS synthesis and detoxification [52, 54].

3. ROS involvement in plant stress responses

The disruption of the equilibrium between the formation of reactive oxygen species (ROS) and antioxidant defense systems, resulting in an unsustainable accumulation of ROS and oxidative stress induction in the plant body, is one of the most imperative effects of environmental stresses. Both enzymatic and non-enzymatic antioxidant defense systems maintain the balance between reclamation and ROS generation when exposed to extreme environmental conditions [57]. Based on their concentration in plants, reactive oxygen species (ROS) can play both harmful and advantageous functions. ROS are unwelcome and dangerous byproducts of natural cellular metabolism at elevated amounts. But, serve as a second messenger in intracellular signaling flows that facilitate a variety of retorts in plant cells at low concentrations. It causes oxidative destruction to lipids, proteins, and DNA, resulting in changes in intrinsic membrane features such as fluidity, ion transfer, enzyme activity loss, protein crosslinking, protein synthesis inhibition, and DNA damage, all of which contribute to cell death. Thus, ROS disrupt biomolecules and cause genetically programmed cell death events at high concentrations. Higher plants have an extensive and very robust plant ROS setup, which is made up of antioxidant enzymes and antioxidant particles, that keeps ROS levels under control to avoid oxidative harm. Environmental factors like heat [58], cold [59], drought [60], Al toxicity [61], organic pollutants (OPs) [62], and pathogens [63, 64] have all been revealed to bring ROS production in plant cells.

On the other hand, changes in ROS levels over time and space are inferred as signals for a variety of biological events, including growth, development, resistance to abiotic stress factors, appropriate response towards pathogen, and cell death. The molecular communication connected with ROS arbitrated signal transduction, which leads to gene expression management, is one of the essential early stress

responses in the plant's acclamatory output. By altering the cell's redox equilibrium, ROS might function as a "second messenger," modifying the actions of particular proteins or gene expression. At any level of plant growth, the network of redox signals composes metabolism to regulate energy generation and consumption, interfering with primary signaling agents (hormones) to respond to evolving environmental nodes. The consequence or fine-tuning of biological reactions to changed ROS levels is determined by interactions with other signaling molecules. Despite the recent identification of several constituents of the ROS signaling system, understanding how ROS-derived signals are incorporated to ultimately control biological processes like plant growth, development, stress adaptability as well as programmed cell death remains a challenge. To offset the negative impacts of oxidative stress, plants engage their antioxidant defense mechanism. Antioxidant defense ability, instead, vary according to plant species and genotype, stress kind, and period of exposure.

3.1 ROS involvement in water stress

Water stress is a common environmental restriction that plants frequently faced during their lives, restricting survival, reproduction, and ultimately productivity. Drought stress causes stomata closing, decrease CO₂ entrance, and compromised photosynthetic rate, as well as discrepancy in the light acquire and usage and changed photochemistry in chloroplasts, triggering ROS excessive formation [49, 65]. The production of reactive oxygen species (ROS), which is assumed to lead to cellular injury, is one of the main and serious alterations due to drought stress. Though, a signaling function for ROS in activating the ROS scavenging mechanism, which might award defence or resistance to stress, has recently been discovered. This scavenging system is made up of antioxidant enzymes including SOD, catalase, and peroxidases, as well as antioxidant substances such as ascorbate and reduced glutathione; the oxidative load is largely governed by the balance between ROS formation and scavenging. Drought stress undoubtedly causes ROS production as a primary plant reaction, which might be regulated by hormones such as ABA and ethylene, which may also perform a downstream function. Unless ROS scavenging by antioxidant systems is disrupted, a high amount of ROS might exacerbate stress made harm to most cellular components [66].

3.2 Plant antioxidant defense against drought

According to Nahar et al. [67], a drought exposed *V. radiate* seedlings had lower AsA/DHA and GSH/GSSG ratios, but higher APX, GR, GPX, and GST activities, compared to control, which added to drought, persuaded oxidative loss tolerance. Rady et al. [68] reported raised H₂O₂ (26.2 percent) and O₂ (51 percent) production, as well as elevated SOD, CAT, and APX activities by 110 percent, 66 percent, and 77 percent, respectively and also considerably amplified AsA, GSH, and -tocopherol level, in *S. Lycopersicum* cv. *Login* 935 treated to drought stress (60 percent FC for 20 days). Improved tolerance for drought stress via the antioxidant framework regulation has also been demonstrated in several chemical priming techniques. Antoniou et al. [69], who found that pre-treatment of *M. sativa* plants with melatonin led to enhanced CAT activity and lower H₂O₂ amount relative to untreated plants.

3.3 ROS involvement in salinity stress

Salinity carries oxidative stress by striking various impediments like ion toxicity, osmotic stress, nutritional deficiency, and toxicity, all of which leading to ROS overproduction and oxidative stress [70].

Rehman et al. [71] identified a 2.5- and 3-fold rise in H₂O₂ generation, as well as a 2- and a 3-fold upsurge in thiobarbituric acid reactive substances (TBARS) concentration, under 100 and 200 mM sodium chloride (NaCl) salinity conditions, respectively, compared to control which exhibits salt-induced oxidative stress.

3.4 Plant antioxidant defense against salinity

Many plant studies have revealed that regulating the antioxidant mechanism reduces the impact of salt stress in various plant species. Researchers have shown that antioxidant enzyme activity varies according to salt level, exposure length, and plant developmental stages [72, 73]. Vighi et al. [74] found a difference in response between salt-tolerant (BRS Bojuru) and salt-sensitive (BRS Pampa) rice cultivars and established that the OsAPX3, OsGR2, OsGR3, and OsSOD3-Cu/Zn genes were the main differentiator markers among these two genotypes. Alzahrani et al. [75] revealed elevated SOD, CAT, GR, and AsA stages in faba bean genotypes, when H₂O₂ levels rose beyond 90% under salinity stress, indicating the control of antioxidant response during salt stress and its alleviation.

Alsahli et al. [76] observed that a 2-fold increase in SOD, CAT, and APX activity and lowered 3-fold H₂O₂ in comparison to untreated control plants when salicylic acid (SA) was applied under salt-stressed in wheat.

Similarly, the antioxidant responses under salt stress conditions were controlled in sour orange through exogenous application of polyamines as reported by Tanou et al. [77], whereas in sorghum with simultaneous treatment of jasmonic acid (JA) and humic acid boosted APX activity, resultant in salt tolerance revealed by Ali et al. [78].

3.5 Plant antioxidant defense against high temperature

Plants' antioxidant defense mechanisms are triggered in response to high temperature (HT) stress [79, 80] although antioxidant capability varies amongst species as well as resistant and susceptible genotypes [81]. Reduced SOD and CAT activity, as well as repressed OsSOD, OsCAT, and OsAPX2 expression resulted in a 1.27-fold increased H₂O₂ accumulation in germinating rice seeds in high-temperature stress, according to Liu et al. [82]. Sarkar et al. [83] discovered increased CAT and POX activities in wheat genotypes during high-temperature stress (30°C).

3.6 Plant antioxidant defense against low temperature

Low-temperature stress causes plants to activate their antioxidant defense appliance to counteract negative consequences. Cucumber (*C. sativus* cv. *Xinyan 4*) seedlings were open to low-temperature stress (15/8°C day/night) for the period of 8 days and reported that 3- and 2-fold increased Cu-ZnSOD and Fe-SOD activities, respectively, in response to increased H₂O₂ and O₂^{*}-production [84]. Besides, after low-temperature stress, *Cynodon dactylon*, *Capsella bursa pastoris*, and *Citrus reticulata* showed considerably enhanced CAT activity [85–87]. Higher APX activity was seen in *Jatropha macrocarpa* in reaction to increase H₂O₂, which enhanced low-temperature stress tolerance, but lower APX activity (>6-fold) in *J. curcas* was connected to enhanced sensitivity under low-temperature circumstances [88]. Cheng et al. [89] studied *Citrullus lanatus* by exposing low-temperature stress (10/5 0C, 7 days) and found that the antioxidant defence system was activated, with GSH/GSSG and AsA/DHA ratios increasing considerably just a day after exposure in comparison to the control trial. Wang et al. [90] reported increased AsA and GSH levels in transgenic apple seedlings under low temperature stress in response to

elevated H₂O₂ concentration (8°C, 12 hours). Han et al. [91] subjected 14-days old rice seedlings to low temperature (12°C, 6 days) stress and found increased H₂O₂ content and O₂^{•-} accumulation, as well as enlarged SOD and CAT activity and also increased GSH/GSSG ratio.

3.7 Plant antioxidant defense against flooding

Numerous crop species have displayed their capability to continue under the flooded or waterlogged situation for brief or even extended durations through triggering antioxidant defense mechanisms. An experiment was conducted by Li et al. [92], using 18 maize genotypes which were subjected to waterlogged conditions and revealed that after 2 days of stress, 12 genotypes had 19–57 percent greater SOD activity, 13 genotypes had 19.16–106.96 percent greater POD activity, and only 9 genotypes had 26–57 percent greater CAT activity. In sesame seedlings under waterlogged conditions, lower AsA content, while higher GSH and GSSG content, as well as H₂O₂ content, was detected in a time-dependent way [93]. During extended (8 days) WL stress, although, AsA-GSH cycle enzymes were not controlled similarly, with considerably increased APX and MDHAR activity and considerably decreased DHAR and GR activity.

Furthermore, Park and Lee [94] found that when the Antarctic plants, *antarctica* was exposed to waterlogged (for 7 days), it accumulated about 52 percent more H₂O₂ and had 91 percent more CAT activity than controls.

3.8 Plant antioxidant defense against toxic metals

Metal toxicity tolerance is favorably coupled with improved antioxidant activity towards ROS detoxification and metal chelation [95, 96]. GST, one of the most important antioxidants, aids GSH in reducing metal toxicity by conjugating with them [97]. GSH also acts as a cytosolic predecessor of phytochelatins (PC), which are metal binders and catalyse the shuttle of metal ions and other xenobiotic that expedites the compound passage into the cell vacuole [81, 98]. The undertaking of cytosolic metals/metalloids ions into the vacuole in passive form lessens cellular toxicity [95]. Furthermore, both GST and GSH play a role in the accumulation of certain flavonoids (anthocyanin), which are metal binders and might follow a similar path to the vacuole [99, 100].

4. ROS generation and removal in the plants

Reactive oxygen species (ROS) are a broad term that includes the radical and non-radical form of species, formed due to incomplete oxygen metabolism. Radical species include superoxide radical (O₂^{•-}), hydroxyl radical (•OH), alkoxyl (RO•) and peroxy (ROO•) while non-radical species contains hydrogen peroxide (H₂O₂), singlet oxygen (1O₂), ozone (O₃), and hypochlorous acid (HClO). Oxygen is a fundamental element found in the Earth's crust that evolved billions of years ago. Oxygen molecules (O₂) are not only crucial for metabolism and respiration but also support life forms on the Earth. O₂ are mainly evolved through the photosynthetic activities of cyanobacteria in ancient times. ROS are partially reduced or activated derivatives of oxygen molecules that are highly reactive and toxic and can cause potential damage to the plants which includes cellular destruction, damage to plant metabolism and growth along with damage to DNA, RNA, proteins, and lipids. Plants perform various metabolic processes viz., namely photosynthesis, respiration which leads to the production of reactive oxygen species in various cell organelles

like mitochondria [7], peroxisomes [8], chloroplasts [6], etc. They are an unavoidable phenomenon that leads to the production of oxidative stress in plants. ROS can also be produced during abiotic and biotic stress responses in plants. Besides this, the presence of free metals (Fe, Cu, Mn) derived from the metallo-protein complex phenomenon also contributes to ROS production. The production of ROS is stimulated by many factors namely physiological responses in the plant cell organelles, hormonal signaling, pathogen attack, gravitropism which produces free radicals inside plants [101]. The stoichiometry of ROS reveals that oxygen contains two unpaired electrons in their outermost shell having similar spin quantum numbers. However, oxygen molecules can accept a single electron at a time in its outermost orbit due to spin restriction, resulting in the formation of ROS which is highly reactive and active in subsequent reactions [102]. ROS are atoms or groups of atoms that possess at least one unpaired electron. Oxygen is an indispensable part of aerobic reactions in the plant system and molecular reduction of O₂ leads to the formation of reactive oxygen species various cell organelles which are highly reactive as of molecular oxygen. Photosynthesis is a crucial metabolic process performed by the plants in the chloroplast of plant cells due to the localization of photosynthetic apparatus in the chloroplast. Although the photosynthetic process is highly influenced by the generation of ROS (O₂.- & 1O₂), the formation of superoxide radicals is associated with PSII. The photolysis of water molecules is a crucial phenomenon in the PSII system of photosynthesis which produces O₂ thus favoring superoxide radical formation reaction in PSI of photosynthesis. Also, auto-oxidation of Iron-sulfur protein results in O₂.- production in the subsequent process due to abundant Fd and low NADP. Furthermore, reduced Fd reacts with superoxide radicals to form H₂O₂ in the illuminated chloroplast [103]. However, the regulation of ROS production during photosynthetic processes has been enunciated in several studies [53, 58, 104]. Singlet oxygen is also produced in PSII during photosynthetic processes. However, the root and stems of rice plants mainly produced O₂.- Which might relate to their subsequent environment for adaptation [105]. Additionally, superoxide radicals can be generated during PSII by auto-oxidation of PSII electron acceptors and PQ [106]. The ROS formation in illuminated chloroplast occurs mainly due to stress conditions followed by the closing of stomata. The partial reduction of O₂ molecule in the respiratory chain occurs in chloroplast which consists of NADPH dehydrogenase and terminal oxidase is termed as chlororespiration. This phenomenon is also a major source of ROS production in the chloroplast. The peroxisomes also mediate the formation of O₂.- through ETC using NADH as an electron donor. Peroxisomes are single membrane-bound organelle that performs certain major functions in the plants like fatty acid β -oxidation, regulation of glyoxylate cycle, photorespiration, metabolism of ROS & ureides, etc. [107–109]. Additionally, peroxisomes also regulate the generation of ROS via various metabolic functions. For instance, H₂O₂ production in the peroxisomes facilitated the regulation of the photosynthetic carbon oxidation cycle in C₃ plants. During the carbon oxidation cycle, oxygenation of RuBP (mediated by RuBisCO) regenerates NADP⁺ and harbors a major sink of electrons which in turn prevents photoinactivation of PSII in the case when CO₂ concentration is lacking. Due to which RuBisCO stimulates oxygenation in place of carboxylation as temperature elevates. The glycolate thus generated by oxygenation of RuBisCO suffers oxidation upon translocation to peroxisomes from chloroplast produces H₂O₂ as a by-product in the cells [102, 110]. Photorespiration is a metabolic process that occurs in chloroplast, mitochondria & peroxisomes. It includes phosphoglycolate metabolism which involves light-dependent O₂ uptake & CO₂ release with peroxisomal glycolate oxidase generating (H₂O₂) in the cells. The mitochondrial metabolism generated a considerable amount of ROS like H₂O₂, hydroxyl radicals, superoxide,

etc. In the plants, mitochondria regulate aerobic respiration includes ETC (electron transport chain), which formulates ROS production in the mitochondrial membrane. However, the mitochondria bestow the limited ROS production in plants possibly due to the presence of alternative oxidase (AOX) that catalyzes the tetra-valent reduction of O₂ by ubiquinone [10]. The series of metabolic reactions in mitochondria leads to the formation of ROS inside the organelle. The flavoprotein region of NADH dehydrogenase encourages the production of O₂⁻ anions during mitochondrial electron transport (MET). One of the effective inhibitors of MET antimycin A enhances the ROS production by blocking electron flow after ubiquinone and the reduced ubiquinone undergoes auto-oxidation by contributing electron to O₂, forming O₂⁻ [111]. Additionally, researchers studied that ubiquinone also contributes to H₂O₂ production in MET [112, 113]. Several mitochondrial enzymes like aconitase and 1-galactono-γ lactone dehydrogenase (GAL) also contribute to ROS generation. Furthermore, the O₂⁻ also gets converted into stable form H₂O₂ by the mitochondrial form of SOD (Mn- SOD). H₂O₂ is further transformed to (OH.) through Fenton reaction which is removed by ascorbate-glutathione cycle enzyme in plant system. Such OH molecules are liable to mutations in ETC of the mitochondrial genome. ROS generation in mitochondria also possesses negative effects on proteins by oxidation, cleavage, degradation of backbones [106]. Mitochondrial dysfunction due to excessive ROS production under unfavorable circumstances induces PCD (programmed cell death) and necrosis in the plants. The respiratory burst oxidase homologue (RBOH) synonymous with membrane-bound NADPH oxidase (NOX) in the plants also contributes to O₂⁻ formation through electron through from intracellular NADPH across the plasma membrane to O₂ in apoplast [103]. NADPH oxidase has a well-established role in stress responses in plants. Neill et al, 2002 studied that RBOH- dependent O₂⁻ generation enunciates lipid peroxidation, PCD. NADPH oxidase induces membrane damage, favors oxidative burst, and reduces plant metabolic and growth-related activities under certain undesirable conditions. The plant cell wall is a site of redox reactions which enables the H₂O₂- dependent reactions and consists of malate dehydrogenase and NADH oxidase. NADPH-dependent microsomal electron transport is also a potential source of superoxides in the plant system. O₂⁻ formation in microsomes is mainly progressed by auto-oxidation of cytochrome P-450 reductase and/or auto-oxidation of oxycytochrome –P-450 complex [114]. Thus, the plant system involves efficient methods of ROS production in different responses. Different cellular compartments enunciate constant ROS production as a byproduct of redox and aerobic reactions. It is interesting to know that under favourable conditions plant maintains redox homeostasis and counteract with ROS production strategies within its system. The system of higher plants is complex and posses various regulatory processes. It is important to understand that controlled ROS generation and oxidative burst can be a fundamental part of the plant signaling and defense mechanism. Future acknowledgments and researches should be directed towards the detailed study of ROS production in various aspects in plants with its signaling implications with references to various molecules present in the plant system. Plants possess a peculiar ROS scavenging system to maintain ROS homeostasis and redox signaling in their system during oxidative stress. However, disrupted protective mechanisms in response to oxidative burst may affect ROS-mediated redox homeostasis and cause cell death in the plants [11]. It is well-acquainted fact that plant produces a considerable amount of ROS during various metabolic processes in several cell organelles like chloroplast, mitochondria, plasma membrane and many more. They are an inexorable part of plant metabolism which play important role in redox signaling under environmental stresses [115]. To accomplish ROS removal from plant system plants consists of several ROS scavenging system which can be

categorized into enzymatic and non-enzymatic defense mechanism. Plants contain various antioxidant enzymes to mediate ROS scavenging mechanism which includes superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), catalase (CAT), monodehydroascorbate reductase (MDHAR or MDAR), dehydroascorbate reductase (DHAR or DAR) and glutathione reductase (GR) (**Figure 2**). These antioxidant enzymes ensure plant survival by minimizing the deleterious effect of ROS and prevent its overaccumulation. SOD (1.15.1.1) is a ubiquitous enzyme that plays a significant role in plant protection against oxidative stress. It catalyzes the dismutation of $O_2^{\cdot -}$ to O_2 and H_2O . SOD has several isoforms and can be categorized as FeSOD, MnSOD, NiSOD, Cu/Zn SOD based on metal cofactors associated with the enzymes. The Arabidopsis genome contains three FeSOD (FSD1, FSD2, FSD3), one MnSOD (MSD1), and three Cu/Zn SOD (CSD1, CSD2, CSD3) type of genes [116, 117]. Similarly, the tomato genome consists of four Cu/Zn SOD, three FeSOD, and one MnSOD [118]. SOD gene family also have been discovered in many plant species like *Musa acuminata*, *Sorghum bicolor*, *Populus trichocarpa*, potato, pea, wheat, etc. However, transgenic approaches have also been described to study SOD responses in plants [10]. SOD isozymes have also been compartmentalized into mitochondria [119], peroxisomes [9], cytosol [116, 120], thylakoids [116, 121]. In plants, SOD is found in roots, leaves, fruits, and seeds where it functions significantly in the environment and oxidative stresses [122], photooxidative stress [123, 124], lateral root growth [119], germination [120], chloroplast development and flowering [121, 125]. Catalases (CAT) (E.C. 1.11.1.6) are a versatile antioxidant that helps in ROS scavenging mechanism in plants. They are

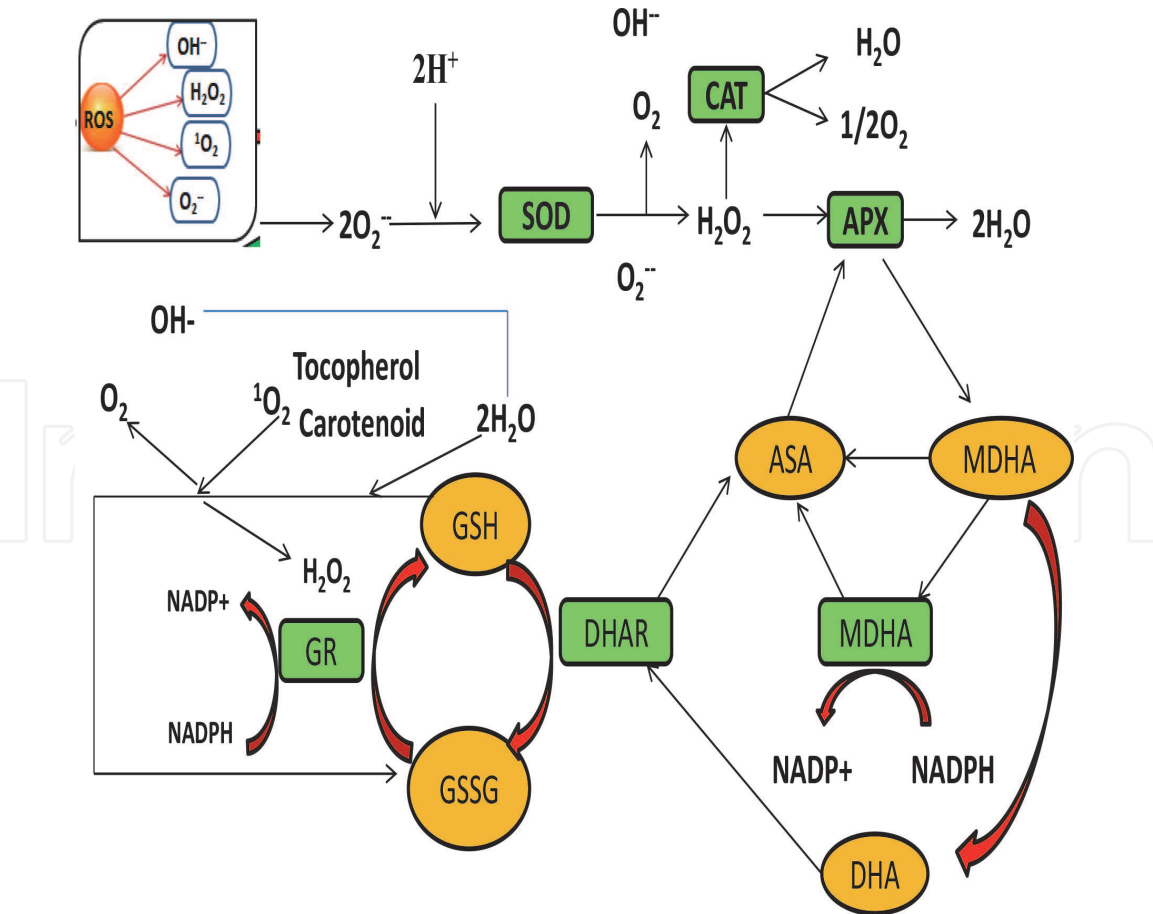


Figure 2. Enzymatic and Non enzymatic Antioxidant mechanism to defend oxidative stress. Enzymatic and non-enzymatic antioxidants in algae. ASC (Ascorbate), APX, (Ascorbate peroxidase), CAT Catalase, DHA Dehydroascorbate, GSH (Glutathione), GR Glutathione reductase, GSSG (Glutathione disulfide), MDHA (Monodehydroascorbate), SOD (Superoxide dismutase), DHA (Dehydroascorbate).

ion containing homotetrameric proteins that catalyze the decomposition of H_2O_2 to H_2O and O_2 during the photorespiration process along with detoxification of H_2O_2 [126]. Catalases are involved in antioxidant defense mechanism have been enunciated in many studies [127–132]. They also mediate in various physiological processes [45, 133–135]. The oxidative stress in plant cells can be maintained by enzymes of ascorbate- glutathione cycle. Ascorbate peroxidase (APX) (E.C.1.11.1.11) is another class of antioxidant enzyme that plays a vital role in scavenging H_2O_2 in chloroplast and cytosol in the plants. They are categorized into various forms based on their localization which is mainly chloroplast stromal soluble form (sAPX), chloroplast thylakoid bound form (tAPX), cytosolic form (cAPX) and glyoxisome membrane form (gmAPX) [136, 137]. They are heme-containing peroxidases possessing nine putative APX genes identified in Arabidopsis in cytosolic, chloroplast and peroxisomal regions of plant cells [138, 139] and sAPX in mitochondria [140]. They detoxify H_2O_2 through electron transfer from ascorbate to form monodehydroascorbate (MDHA). APX possesses several metabolic functions in H_2O_2 scavenging, plant responses to environmental stress, photoprotection, and plant development [115]. Another enzyme of ascorbate- glutathione cycle MDHAR (E.C.1.6.5.4) catalyzes the reverse reduction of MDHA to ascorbate in the presence of NAD(P)H [141] Foyer & Noctor, 2011). MDHAR is mainly localized in the cytosol, peroxisomes, mitochondria, and chloroplast. MDHAR is involved in stress tolerance, plant physiological processes, senescence, interaction, with endophytes has been explored in various studies [115, 142, 143]. DHAR is another enzyme that brings about the regeneration of ascorbate from DHA. DHARs (E.C.1.8.5.1) are monomeric enzymes that are identified in the Arabidopsis genome as DHAR1 and DHAR2 (cytosol), DHAR3 (chloroplast) [144]. Similar to APX, DHAR is also involved in the regulation of defense against environmental stress in various species [145, 146]. Glutathione reductase (GR) (E.C.1.6.4.2) is another potent enzyme mainly localized in chloroplast, mitochondria and cytosol. It catalyzes the reduction of glutathione and contains FAD-binding domain & NADPH- binding domain which carries out an enzymatic activity. Isozymes of GR have been widely studied in Arabidopsis which plays a vital role in various plant physiological responses [115].

The non-enzymatic antioxidant defense mechanism includes several low molecular mass ROS scavenging molecules like glutathione, ascorbic acid (AsA), flavonoids, carotenoids, tocopherols, alkaloids which aid in the removal of H_2O_2 , singlet oxygen, and other ROS molecules. The antioxidant defense mechanism of AsA during oxidative burst has been well acquainted through several studies. AsA (commonly known as Vit C) is water-soluble, localized in many plant cell organelles stimulates the quenching superoxide hydroxyl radicals and singlet oxygen produced during oxidative stress. Despite these, it also reduces H_2O_2 to H_2O via ascorbate peroxidase reaction [147]. AsA regulates antioxidant defense mechanisms in response to various environmental stresses [148]. The non-enzymatic antioxidant system functions along with an enzymatic system to counteract the negative effect of ROS in plants. Reduced glutathione (GSH) is another class of low M.W thiol tripeptide antioxidant molecule commonly dominated in the cytosol, ER, mitochondria, chloroplast, vacuoles, peroxisomes & apoplast. GSH mediates multiple functions in plants. It plays a vital role in plant physiological functions like cell differentiation, growth, senescence, and many more. Precisely, it is also known for its antioxidant defense system in oxidative stress. It scavenges H_2O_2 , 1O_2 , $\text{OH}\cdot$, $\text{O}_2\cdot^-$, and reduces them to produce GSSG as a by-product. GSSG can also be generated through GSH. GSH plays a crucial part in regenerating AsA via the ascorbate- glutathione cycle. GSSG gets converted to GSH through denovo synthesis or by GR. Similar to glutathione another potential antioxidant molecule also

includes proline, amino acids, alkaloids, polyamines, terpenes, amines, phenolics like compounds that scavenge ROS in plants. Carotenoids, on the other hand, are a group of lipophilic antioxidants that are present in a wide variety of organisms including plants. They have a well-established role in photosynthesis and protect photosynthetic machinery in response to ROS production. They scavenge 1O_2 , thus preventing generation by reacting with $3Chl^*$ and excited Chl (Chl^*), regulates the xanthophylls cycle. Similar to carotenoids, α -tocopherol is also a protector of the cell membrane in response to ROS production. α -tocopherol quench excess energy, safeguard lipids, and scavenges ROS formed during photosynthesis. It usually reacts with lipid radicals $RO\cdot$, $ROO\cdot$. And RO^* at membrane- water interface and gets reduced to TOH. Which is then interacts with GSH & AA [149]. Flavonoids like flavonols, flavones, isoflavones, and anthocyanins are diverse in the plant kingdom and also plays a crucial role in the various physiological process mainly pigmentation in flowers, fruits, and seeds. They mitigate the negative effects of ROS produced in plants during photosynthesis. Additionally, they also scavenges 1O_2 along with repairing chloroplast membrane [150].

5. ROS regulation with genes and tolerance to abiotic stress tolerance in crops

Plants are evolved with multiple signaling pathways to control various sets of genes for generating different classes of protein to cope up with abiotic stress. These highly regulated genes play a very important role in ROS activation and regulation. Functional genomics helps us to identify more than 1000 stress-responsive genes in plants [151]. These genes have been characterized into different classes such as protein kinases and phosphatases, transcription factors, enzymes, molecular chaperones, and other functional proteins. The different genes involved in the regulation of ROS homeostasis and response to abiotic stresses have been categorized in plants (Figure 3; Table 2).

5.1 Protein kinases and phosphatases

Mitogen-activated protein kinases (MAPK) are the important gene groups in ROS signaling and regulation. Many studies have been conducted in plants on MAPK cascades [174]. In cotton, two MAPK kinases (MAPKKs) have been characterized (GhMKK1 and GhMKK5) which are responsible for the homeostasis of ROS and abiotic stress tolerance [152]. Due to overexpression of GhMKK1 in tobacco, tolerance to salt and drought stresses have been observed by exhibiting ROS scavenging along with activities of antioxidant enzymes [175]. In transgenic tobacco plants, when BnMKK1 gene has been introduced, it triggers ABA signaling and leads to drought sensitivity and water loss [158] whereas GhMKK5 gene reduces salt and other abiotic stresses [152]. Plants showing overexpression of GhMKK5 leads to the up-regulation of ROS-related genes resulted in hypersensitive reaction with an accumulation of H_2O_2 [176]. In another study, a gene called GhMKK3 helps in regulating drought tolerance. Overexpression of this gene in tobacco induces stomatal closure due to activation of ABA-responsive gene along with a reduction in stomatal numbers [153, 177]. In some cases, two or more genes (GhMKK3 and HgPIP1) work together in connection with HgMPK7 gene for the production of drought and ABA-activated MAPK modules [178]. A drought-hypersensitive mutant1 (DSM1) of MAPK gene has been identified in rice which shows the sensitive response to oxidative stress [154]. In rice plants, two calcium-dependent protein kinase (CDPK) genes, OsCPK12 and OsCPK4 enhance tolerance to salt and

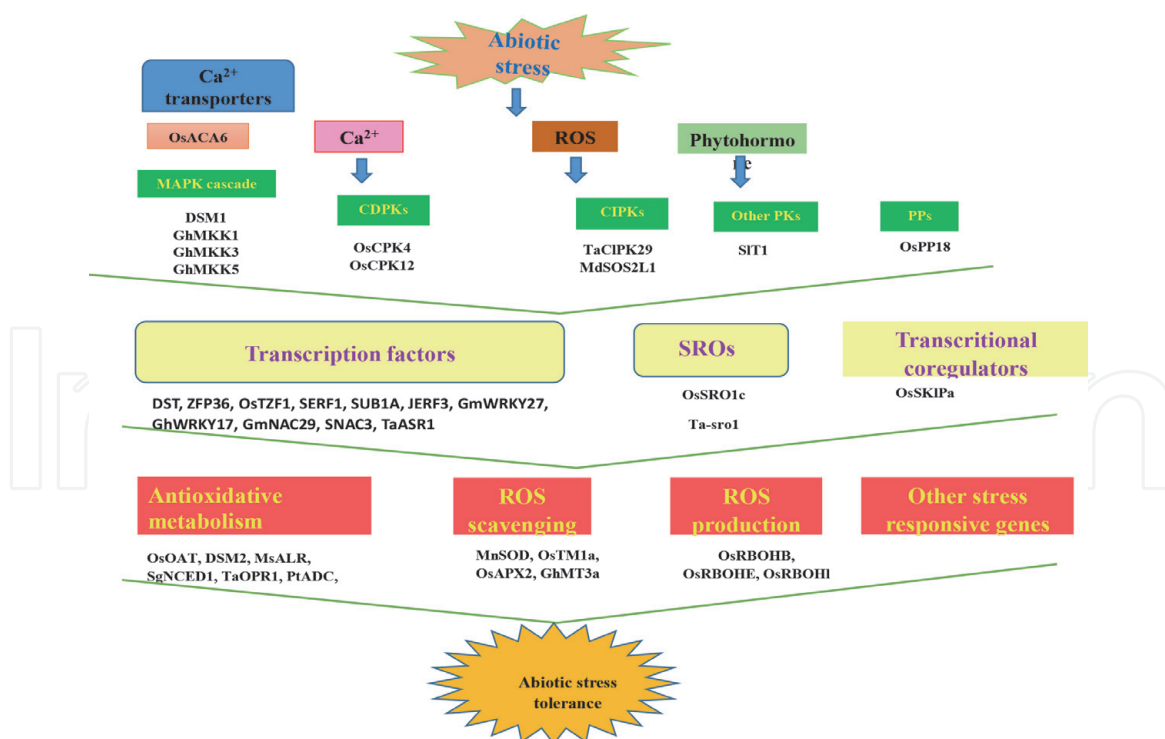


Figure 3. Representative diagram showing several major genes/factors involved in ROS regulation and provides abiotic stress tolerance response in plants. Abbreviations: calcium-dependent protein kinase (CDPK); calcineurin B-like protein-interacting protein kinase (CIPK); mitogen-activated protein kinase (MAPK); protein kinase (PK); similar to RCD one (SRO).

drought stress respectively [155]. CBL-interacting protein kinase (CIPK) gene TaCIPK29 in wheat also is salt tolerance with ROS regulation mechanism (Table 3).

In transgenic tobacco, activities of ROS- scavenging enzymes have been increased along with the expression of transporter genes which leads to abiotic stress (salt stress) tolerance [156]. Another CIPK gene (MdSOS2L1) showed abiotic stress (salt tolerance) tolerance in crops like tomato and apple. Increased antioxidant metabolites (malate, procyanidin) and ROS scavenging enzymes are the mechanisms found after molecular characterization of MdSOS2L1 gene [157]. In many cellular functions, protein phosphatase plays a crucial role in signal transduction with a process called dephosphorylation. A protein phosphatase gene, OsPP18 (PP2C) has been identified in rice crops, which shows drought resistance response via ABA-independent pathways and regulating ROS homeostasis [158]. PPC2 genes have been identified and characterized in the genome of *Medicago truncatula* [201]. Genome studies in Brassica [202] maize, tomato, and Arabidopsis also indicated the presence of PP2C gene families, responsible for abiotic stress tolerance [203, 204]. Among the two subfamilies of PP2C, subfamily A is used in ABA-dependent stress responses and B subfamily is MAPK regulators [205].

5.2 Transcriptional factors

Transcriptional factors (TFs) play an important role as a regulatory protein that could change the expression of stress-responsive genes and enhance tolerance to abiotic stress in plants. There are many studies on transcription factors that show their role in abiotic stress management in plants [206–208]. In-plant abiotic stress responses, members of AP2/ERF, zinc finger, NAC, and WRKY families have been identified and characterized to play a major role in the regulation of ROS homeostasis [209–211]. AP2/ERF (APETALA2/ethylene response factor) group of transcription factors regulates various abiotic stress responses and are found in certain

Functional Class	Functional Protein	Genes involved	Plant concern	Abiotic Stress Resistance	ROS regulation	Reference
Protein Kinase and phosphatase						
MAPKs	MAPKK	<i>GhMKK1</i>	<i>G.hirsutum</i>	Drought and salt stress	ROS scavenging	[152, 153, 175]
	MAPKKK	<i>DSM1</i>	<i>O. sativa</i>	Drought stress	ROS scavenging	[154]
CDPK	Calcium-dependent protein kinase	<i>OsCPK12</i>	<i>O. sativa</i>	Salt stress	ROS production and scavenging	[155]
	Calcium-dependent protein kinase	<i>OsCPK4</i>	<i>O. sativa</i>	Drought and salt stress	ROS scavenging.	
CIPK	CBL-interacting protein kinase	<i>TaCIPK29</i>	<i>T. aestivum</i>	Salt stress	ROS scavenging	[156]
	CBL-interacting protein kinase	<i>MdSOS2L1</i>	<i>Malus x domestica</i>	Salt stress	ROS scavenging; antioxidative metabolism	[157]
Protein phosphatase	Protein phosphatase 2C	<i>OsPP18</i>	<i>O. sativa</i>	Drought and oxidative stress	ROS scavenging	[158]
Transcription factors						
AP2/ERF	ERF	<i>SERF1</i>	<i>O. sativa</i>	Salt stress	ROS signaling	[159]
	ERF	<i>SUB1A</i>	<i>O. sativa</i>	Drought, submerge and oxidative stress	ROS scavenging	[160]
	ERF	<i>JERF3</i>	<i>S.lycopersicum</i>	Drought, salt and freezing stress	ROS scavenging	[161]
Zinc finger	C2H2 zinc finger	<i>DST</i>	<i>O. sativa</i>	Drought and salt stress	ROS scavenging	[162]
	C2H2 zinc finger	<i>ZFP36</i>	<i>O. sativa</i>	Drought and oxidative stress	ABA-induced antioxidant defense	[163]
	CCCH zinc finger	<i>OsTZF1</i>	<i>O. sativa</i>	Drought, salt and oxidative stress	ROS scavenging	[164]
NAC	NAC	<i>GmNAC29</i>	<i>G. max</i>	Drought and salt stress	ROS production	[165]
	NAC	<i>SNAC3</i>	<i>O. sativa</i>	Drought, heat and oxidative stress	ROS scavenging	[166]
WRKY	WRKY	<i>GmWRKY27</i>	<i>G. max</i>	ROS production	Drought and salt stress	[165]

Functional Class	Functional Protein	Genes involved	Plant concern	Abiotic Stress Resistance	ROS regulation	Reference
	WRKY	<i>GhWRKY17</i>	<i>G. hirsutum</i>	ROS scavenging	Drought and salt stress	[167]
Other nuclear proteins						
SRO protein	SRO	<i>OsSRO1c</i>	<i>O. sativa</i>	Drought and oxidative stress	ROS scavenging	[168]
	SRO	<i>Ta-sro1</i>	<i>T. aestivum</i>	Osmotic, salt and oxidative stress	ROS production and scavenging	[33]
ABA metabolism	Carotene hydroxylase	DSM2	<i>O. sativa</i>	Drought and oxidative stress	antioxidative metabolism	[169]
	9-cis-epoxycarotenoid	<i>SgNCED1</i>	<i>S. guianensis</i>	Drought and salt stress	ABA-induced antioxidant defense	[170]
ROS scavenging	MnSOD	<i>MnSOD</i>	<i>N. plumbaginifolia</i>	Drought stress	ROS scavenging	[171]
	APX	<i>OsAPX2</i>	<i>O. sativa</i>	Drought, salt and cold stresses	ROS scavenging	[172]
Calcium transporters	type IIB Ca ²⁺ ATPase	<i>OsACA6</i>	<i>O. sativa</i>	Drought and salt stress	ROS scavenging	[173]

Table 2.
Major representative genes of crops involves in abiotic stress tolerance through ROS regulation.

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
For salt stress plants are applied 12 dS m ⁻¹ NaCl after 2 weeks of germination	Pot	Maize	Se application (20 mg/L)	Improved shoot fresh and dry weight compared to control	[179]
For salt stress each pot pre-treated with 150 mM of NaCl for four weeks before AM fungus treatment	Pot	Rice	AM fungus <i>Claroideoglomus etunicatum</i> (isolate EEZ 163) @ 700 infective propagules per pot at sowing time just below rice seedlings	Significantly ↑ shoot dry weight (156%), root length (63%) under 150 mM NaCl concentration compared to uninoculated control plants	[180]
For salt stress seedling are dip into Hoagland's medium containing 200 mM salt solution	Pot	Wheat	Seedling allowing in Hoagland's medium containing 200 mM salt solution and 5 ml PGP bacterial solution (<i>Bacillus</i> sp. (EN1), <i>Zhihengliuella</i> sp. (EN3), <i>S. succinus</i> (EN4), <i>Bacillus gibsonii</i> (EN6), <i>Oceanobacillus</i> sp. (EN8), <i>Halomonas</i> sp. (IA), and <i>Thalassobacillus</i> sp. (ID), <i>Halobacillus</i> sp) @ 1 × 10 ⁹ cfu mL ⁻¹	Significantly ↑ growth rates of the plants are 67.5%, 64.4%, 62.2%, 76.3%, 70.6%, 73.5% and 78.1% for EN1, EN3, EN4, EN6, EN8, IA and ID as well as ↑ total fresh weight and length of root and shoot of wheat seedlings compared to control	[181]
Irrigated by saline water with 5 salinity levels: S1: 2 dS m ⁻¹ , S2: 4 dS m ⁻¹ , S3: 6 dS m ⁻¹ , S4: 8 dS m ⁻¹ , and S5: 10 dS m ⁻¹	Pot	Tomato	Nano-fertilizer consisting of 79.19% CaCO ₃ and 4.62% MgCO ₃ % are applied through foliar spraying in three concentrations: N1: 0.5 g L ⁻¹ , N2: 0.75 g L ⁻¹ , and N3: 1 g L ⁻¹ .	Significantly ↑ average number of clusters and flowering, fruit set (especially in N1/S1: 65%), yield of fruit compare to control (N0/S1: 26% fruit set)	[182]
Marigold seedlings were exposed to four levels of drought stresses (100% (D ₀), 75% (D ₁), 50% (D ₂), and 25% (D ₃) according to	Pot	Marigold	The inoculum (5 g of soil containing spores of AM fungi <i>Glomus constrictum</i> Trappe) are placed 3 cm below the surface of the soil (before	Significantly ↑ plant height (7.7, 4.9, 5.5 and 16.2%), dry weight of shoot (19.14, 25.6, 5.88 and 31%) and flower (42.6, 9.6 and 21.8%,	[183]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
water holding capacity of the soil			sowing) to produce mycorrhizal pants	respectively) compared to non-AM inoculated plant	
For water stress plants are supplied 50%, 75%, 100% water after germination	Pot	Sorghum	Surface sterilized seeds are dipped in inoculums (<i>Streptomyces laurentii</i> EU-LWT3-69 and <i>Penicillium</i> sp. strain EU-DSF-10) for 2 h and sown in pot	Significantly ↑ plant root and shoot length, dry weight of biomass compared to uninoculated plants	[184]
Exposure of inoculated plant to a 8-week drought-stress	Pot	Timothy (Phleum pratense L.)	At 3 weeks post seeding, each seedling was inoculated by pipetting 0.5 mL of phosphate buffer containing 10 ⁶ CFU of <i>B. subtilis</i> strain B26	Significantly ↑ in shoot and root biomass by 26.6 and 63.8% compared to uninoculated plants	[185]
For salt stress, 150 mM NaCl applied after 5 weeks of transplantation or at 5 to 6 leaf stage, and For drought stress, plant supplied of half of the water required for normal irrigation	Pot	Cucumber (<i>Cucumis sativus</i>) (cv. Cador, cv. Venus)	Foliar spray with Si (2.25 mM) as K ₂ SiO ₃ to stressed plant at 10 days interval	Significantly ↑ in the R/S ratio by > 20 % in Cador and about 15 % in Venus cultivars	[186]
For flooding stress, 8 weeks older plants are flooded with deionised water for 15 days	Pot	<i>Ocimum sanctum</i>	Seedling treated with ACC deaminase-containing rhizobacteria bacterial inoculum of Fd2 (<i>Achromobacter xylosoxidans</i>), Bac5 (<i>Serratia ureilytica</i>), Oci9 (<i>Herbaspirillum seropedicae</i>) and Oci13 (<i>Ochrobactrum rhizosphaerae</i>) @ 10 ⁸ CFU/ml before imposing stress	Significantly ↑ in fresh weight Fd2 (46.5%) followed by Oci13 (45.1%), Bac5 (26.5%) and Oci9 (16.6%), root weight in Fd2 (37%), shoot length 76.3, 41.1, 31.3 and 19.7%, number of leaves is 41.9, 37.7, 16 and 11%, number of nodes in Fd2 (72%) Bac5 (66%), Oci9 (33%) and Oci13 (27%) respectively.	[187]
For flooding stress, 5 month older plants are induced flooding/	Pot	Muscadine Grape (<i>Muscadinia</i>	control (aerated plants), aerated + Si (250 ppm), aerated + SiNP	Si significantly ↑ the dry weight of root, shoot, and total weight 20,	[188]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
hypoxia stress by limiting the oxygen supply to the nutrient solution in hydroponic units		<i>rotundifolia</i> Michx.)	(250 ppm), hypoxia stress, hypoxia stress + Si (250 ppm), and hypoxia stress + SiNPs (250 ppm)	30 and 15%, Si + hypoxia stress ↑ 125, 120 and 125%, SiNPs + control ↑ 30, 46 and 20% and overall improvement is 155% compared to untreated control	
Heat stress treatment imposed on plants after 4 weeks of emergence and raised temperature by 2° C each day to avoid osmotic shock until the desired temperature level (45±2°C) are achieved	Pot	Tomato	Plants are sprayed 45 days after sowing with sulphur (S) @ 2, 4, 6, and 8 ppm for 2 times at 15 and 22 days after heat induction	In thermo tolerant cultivar @ 6 ppm S significantly ↑ maximum shoot (38.3 cm) and root (12.3 cm) length, shoot fresh (46.65g) and dry (14.57g) weights, average root fresh (12.21g) and dry (6.44g) weight, and in thermo sensitive cultivar fresh weight of fruit (42.1g), shoot fresh (42.14g) and dry (13.16g) weight, root fresh (12.21g) and dry (5.3g) weight compared to @ 2, 4, 8 ppm and untreated control	[189]
Heat stress treatment in Pot: at squaring, flowering and ball formation Field: April (medium temperature), early May (high temperature) and mild-June (optimum temperature) at squaring, flowering and boll formation stage	Pot and field	Cotton	Foliar spray of K, Zn and B @ 1.5, 0.2 and 0.1 % one day before heat treatment	Pot: Significantly ↑ seed cotton yield (SCY) in K (21%) Zn (16%) and B (7%) and average ball weight compared to control Field: Significantly ↑ seed cotton yield (SCY) in April (15%) and May (17%) thermal regimes and average ball weight compared to control in both year	[190]
For heat stress treatment at V ₃	Pot	Soybean	2 days after transplantation,	Significantly ↑ in shoot length	[191]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
stage plants are exposed for 5 and 10 days			50 ml of freshly diluted <i>Bacillus cereus</i> SA1 culture (10^9 CFU/mL) are inoculated to each pot and repeated further 2 times after 5 days	(15.08%), root length (14.63%), fresh and dry weight (27.28 and 12.39%, respectively) after 5 and similar pattern followed by 10 days	
1 week after bacterial drench treatment, each pot are watered with 20 ml tap water and then heat and drought stressed by withholding watering for 5-7 days at 35°C in a growth chamber	Pot	Chinese cabbage	Seedlings (four-leaf stage) were drenched with bacterial suspensions (<i>Bacillus aryabhatai</i> H26-2 and H30-3) @ 10^7 cells/ml, 1 ml/g of potting mixture	Significantly ↑ in fresh weight (2.4% in H30-3) and number of lateral root (10.95 and 1.5% in H30-3 and H26-2, respectively) compare to control	[192]
For drought stress pots are irrigated with 80, 60 and 40% of water holding capacity for 60 days	Pot	Common bean (<i>Phaseolus vulgaris</i> L)	Before sowing seeds are treated with H ₂ O ₂ for 4 hour	Significantly ↑ in root (8.15, 2.72%) and shoot (21.09, 10.52%) length, root fresh (25, 10%) and dry (31.25, 15.38%) weight, shoot fresh (21.12, 6.6%) and dry (21.68, 5.79%) weight in 60 and 40% WHC, respectively.	[193]
Drought stress induced in the pots artificially by irrigating the pot with a PEG-6000 (g/L of water) nutrient solution	Pot	Black gram and garden pea	Seed treatment with bacterial inoculum in individual with RJ12, RJ15 and RJ46 and in consortium with RJ12 + RJ15, RJ12 + RJ46, RJ15 + RJ46 (1×10^8 CFU ⁻¹)	Significantly ↑ in germination percentage (3-13, 7.7-17%), root length (21.15-55, 48.27-64.7%) and shoot length (26.66-35.67, 13.33-22.15%) varies in both crop plant respectively	[194]
For cold stress treatment pot are kept at 8±2°C for 60 days	Pot	Wheat	Seed treatment with charcoal based inoculum of the bacterial (<i>Pseudomonad</i>) culture 10^8 cfu g ⁻¹	Significantly ↑ in shoot (4.7-26.1%), root length (27.9–70.5%), root (1.04–2.04-fold), and shoot biomass (1.25–1.66-fold) as compare to control	[195]

Stress condition	Experimental condition	Plant sp.	Management strategy	Result	Reference
For cold-stress 40 day old seedlings are transferred at 15/10°C (day/night) for two weeks	Pot	Cucumber	Each pot inoculated with 10 g of the AM fungi <i>R. irregularis</i>	Significantly ↑ shoot (7%) and root (25%) dry matter per gram compared to control	[196]
Heavy metal stress of Cadmium ($\text{CdSO}_4 \cdot 8\text{H}_2\text{O}$) treatments (0, 100 and 200 mg/l)	Pot	Mustard	SA (1.0 mM) are sprayed in the evening (10 ml/plant) to plants mixed with tween-20 every alternate day from the 1st day of treatment up to day 45	Significantly ↑ shoot (7%) and root (5%) fresh weight and Shoot and root dry weight (5%) @ 200 mg/l and 1 mM SA concentration compared to control	[197]
For heavy metal stress of Cr, plants after 30 days of germination, both soil and sand pots are irrigated with Cr as $\text{K}_2\text{Cr}_2\text{O}_7$ solution (500 ml pot^{-1}) of 0, 0.25, and 0.5 mM in 7-day interval	Pot	Wheat	Glycinebetaine in 0.1 % Tween-20 solution are applied at 0 and 100 mM on the leaves until runoff at both tillering and booting vegetative stages	Significantly ↑ plant height, root length, kernel length, and number of tillers per plant compared to control	[198]
For heavy metal stress of Hg, seedlings are treated with HgCl_2 at 60 and 100 μM concentration for 7 days	Pot	Rice	Application of different combination with HgCl_2 of SNPs @ 100, 200 μM or KNO_2 @ 200 μM or $\text{K}_4\text{Fe}(\text{CN})_6$ @ 200 μM or TIBA 1 μM	Significantly ↑ shoot and root length compare in all treatments to Hg treated plant	[199]
For heavy metal stress of Al, plants are treated with Al (500 μM) + salicyclic acid at different concentration for 2 weeks in Hoagland solution	Pot	Tomato var. SIRI and GOWRI	Application of salicyclic acid (SA) @ 100, 250 and 500 μM concentration on seedling which is mix in Hoagland for 2 weeks	Significantly ↑ plant growth in SIRI (65-85%) and GOWRI (20-55%)	[200]

Table 3.
Various management options to control various abiotic stresses in plants

rice varieties. They can acclimatize in stress conditions and minimize the energies consumed via gibberellin and ethylene responsiveness [212]. Although in the early stage of abiotic stresses, ROS levels act as an adaptation signal but the key components of ROS signaling are still unknown. In rice, ERF transcription factor SERF1 plays a very important role in molecular signaling (H_2O_2 mediated response) during the resistance response against salinity tolerance [159]. Another factor SUB1A

reduces gibberellin response and ethylene production in submerged rice genotypes and conserves carbohydrates for future use. After the flooding subsides, plants go through severe leaf desiccation [204] which leads to ROS accumulation in plant tissues [206]. SUB1A boosts submergence tolerance by activating ROS-scavenging genes and also induces ABA responsiveness while activating stress genes [160, 213]. The JERF3 gene was also found to be involved in abiotic stress tolerance in tomato (*S. Lycopersicum*) by modulating ROS regulation and also influence the expression of genes involved in oxidative, osmotic stress responses which ultimately reduces ROS accumulation [161].

Zinc finger domains(s) were reported to be one of the most important transcription factors used in ROS regulation for abiotic stress tolerance in Arabidopsis and other plant species [214]. Based on the location and number of protein residues, zinc finger proteins are classified into several groups such as C2H2, CCCH, C2C2, and C3HC4 [211]. Gene DST accumulates H₂O₂ in the guard cell of the rice plant and enhances abiotic stress (drought and salt) tolerance while increasing the closure of stomata [162]. In rice crops, two other zinc finger proteins (ZFP179 and ZFP36) also help in the regulation of ROS homeostasis and abiotic stress tolerance [215, 163]. Another protein OSTZF1 enhances the expression of ROS-scavenging enzymes and genes responsible for redox homeostasis which helps in modulating abiotic stress resistance [164].

TF families also include the NAC group, which is one of the largest TF families with approximately 300 members among rice and Arabidopsis [216, 217]. This group of TFs helps in abiotic stress tolerance through ROS regulation. In Soybean, GmNAC2 transcription factor involves in signaling pathways of ROS and modulate the expression of ROS-scavenging genes [218]. Another NAC TF gene-SNAC3 has been identified in rice crops which regulates positively during drought stress and high temperature enhances abiotic stress tolerance by controlling ROS-related enzymes [219].

Another TF family WRKY is widely involved in Arabidopsis and Rice which has more than 100 genes only in these two plants [208]. These WRKY genes regulate both biotic and abiotic stress responses [220]. The WRKY transcription family is consists of a highly conserved region WRKYGQK heptapeptide at the C terminus and at the N- terminus a zinc-finger motif is present. These WRKY domains bind to W-box in the promoter regions and regulate various physiological responses [201, 221]. In rice WRKY genes reduces the oxidative stress tolerance effects by enhancing ROS and ABA functions. In transgenic soybean, the GmWRKY27 gene enhances drought and salt tolerance response by reducing ROS levels [165]. Another WRKY gene-GhWRKY17 in cotton involves abiotic stress tolerance by regulating ROS level and also by modifying ABA signaling pathways [167].

5.3 SRO proteins

SRO proteins which are also known as SIMILAR TO RCD ONE, are characterized as plant-specific proteins. Their domain characterization shows that they contain a C-terminal RCD1-SRO-TAF4 (RST) domain, N-terminal WWE domain, and a poly (ADP-ribose) polymerase catalytic (PARP) domain. In rice, the OsSRO1c gene targets abiotic stress (drought) related transcription factor (SNAC1), accumulates H₂O₂ in plant cells which leads to a reduction in water loss by reducing stomatal aperture [168]. OsNAC5 and ONAC095 have also been found to enhance drought and oxidative stress tolerance in rice [7]. In wheat crops, overexpression of the Ta-sro1 gene helps in cellular homeostasis with the regulation of ROS (through ROS-mediated enzymes) and provides salinity tolerance [208].

5.4 ABA metabolism-related proteins

Abscisic acid (ABA) plays an important role as a phytohormone that induces abiotic stress tolerance response in plants. In rice during drought condition, mutant gene *dsm2* have been identified which synthesize β -carotene hydroxylase which is a precursor of ABA. Overexpression of *DSM2* enhances stress-related ABA-responsive gene expression and increases xanthophylls which lead to resistance response in abiotic and oxidative stresses [169]. In ABA catabolism, another hydroxylase-encoding gene-*OsABA8ox3* is involved and controls oxidative stress under abiotic stress conditions [209]. In transgenic tobacco plants, overexpression of the *SgNCED1* gene (9-*cis*-epoxycarotenoid dioxygenase gene from *Stylosanthes guianensis*) increases ABA content and provides tolerance response to salt and drought stresses. This tolerance response is associated with the inducing production of NO and H₂O₂ along with the activation of ROS-scavenging enzymes [170].

5.5 ROS-scavenging proteins/enzymes

The presence of ROS-scavenging enzymes such as SOD, APX, and CAT in every cellular compartment of crop plants helps in ROS detoxification and protects against several abiotic stresses [52]. In water scarcity condition, improved yield and survival rate is observed in transgenic alfalfa crop due to the presence of MnSOD gene [171]. In transgenic rice plants under cold stress conditions, APX gene-*OsAPX1* shows an increased percentage of spikelet fertility whereas overexpression of *OsAPX2* gene increased drought stress tolerance as compared with wild-type plants [172].

5.6 Ca²⁺ transporters and binding proteins

For the growth, development, and stress tolerance in plants, Calcium (Ca²⁺) controls several signaling pathways. P-type Ca²⁺ATPases or antiporters maintain the basal cytosolic level by regulating the influx and efflux of Ca²⁺ across the membranes. In rice crops, *OsACA6* gene has been isolated and characterized. In tobacco plants, overexpression of the *OsACA6* gene reduces ROS accumulation and induces expression of stress-responsive genes which leads to drought and salinity tolerance [173]. In transgenic lines, this gene controls cellular ion homeostasis and ROS-scavenging pathways which give tolerance response to Cd²⁺ stress [222].

6. Conclusion and future prospects

In the field of plant stress and ROS production, key sources, mechanism and various antioxidant enzymes to counteract the ROS are well reported. However, ROS homeostasis, signal transduction and interaction among various cellular compartments towards signaling are largely unknown and need to be addressed. Many studies reported that many antioxidant remain involve in ROS regulation but their inter and intra compartmental coordination to adjust ROS during stress condition is poorly understood. Therefore, to develop a conceptual and comprehensive framework, a combination of transcriptome, proteome, and metabolome approaches is required to understand ROS development, signaling pathways and their management.

Plants need robust and comprehensive adaption mechanisms to combat under stress conditions. For better stress resistance and ROS homeostasis many specific genes responsible for stress resistance has been identified in rice and transgenic

plants. However, most of the ROS associated genes are studied for the expression of antioxidant enzymes activity and large field scale testing of transgenic plants for stress tolerance is very limited. Thus, in order to improve the abiotic stress tolerance by homeostasis of ROS, functions of associated genes and mechanism to control the ROS signaling pathways require detailed investigation. In future, these ROS associated genes and QTLs can be used in breeding and genetic engineering programme for the development of abiotic stress resistance cultivar.

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